

NOTES ON LIFE HISTORIES AND DESCRIPTIONS OF ADULTS AND
IMMATURE STAGES OF *PROCECIDOCHARES KRISTINEAE* AND *P. LISAE*
NEW SPECIES (DIPTERA: TEPHRITIDAE) ON *AMBROSIA* SPP. IN
SOUTHERN CALIFORNIA

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Abstract.—*Procecidochares kristineae* Goeden, n. sp., and *P. lisae* Goeden, n. sp., are described and figured as adults and distinguished from each other by their wing patterns, chaetotaxy, and genal color and by these and additional characters from all other North American congeners. Sexually dimorphic wing patterns in *P. lisae* are reported for the first time from this genus. First through third-instar larvae and puparia also are described and figured for both species, but few morphological differences were found. *Procecidochares kristineae* and *P. lisae* are strictly monophagous tephritid flies forming axillary bud galls on branches of the native, shrubby, xerophytic ragweeds, *Ambrosia dumosa* (Gray) Payne and *A. eriocentra* (Gray) Payne (Asteraceae), respectively. Both are circumnata species that overwinter as first instars within incipient galls in southern California. Further gall and larval development and host-plant regrowth and reproduction are stimulated concurrently by winter rainfall. Reproduction by *P. kristineae* is rarely biennial, usually univoltine or bivoltine, and rarely trivoltine, depending on local yearly rainfall patterns; whereas, *P. lisae* usually is univoltine or bivoltine.

Key Words: Insecta, *Procecidochares*, *Ambrosia*, ragweed, biology, galls, taxonomy of adults and immature stages, sexual dimorphism, parasitoid

Two undescribed species of *Procecidochares* (Diptera: Tephritidae) were detected during faunistic surveys of native ragweeds, *Ambrosia* spp. (Asteraceae: Ambrosiinae), in southern California by Goeden and Ricker (1976a, b). The life history of one species forming galls on *A. dumosa* (Gray) Payne was studied by Silverman and Goeden (1980), but it has remained unnamed until now. In this paper, both tephritid species are named, their adult and immature stages are described and illustrated, and new life-history information on each is reported.

MATERIALS AND METHODS

Our field studies on the tephritid infesting *A. dumosa* were conducted near sea lev-

el in the low-elevation Colorado Desert (= northern Sonoran Desert) in southern California (Munz 1974) at various locations in Imperial, Riverside, and San Diego counties listed by Silverman and Goeden (1980) or mapped by Goeden and Ricker (1976a). Our principal study site for the fly on *A. eriocentra* (Gray) Payne was Mountain Pass at 1430-m elevation, San Bernardino Co., in the high-elevation, Mojave Desert; although this tephritid also was reared from galls obtained from surrounding locations named below in northeastern San Bernardino Co. during 1970-71 faunistic surveys (Goeden and Ricker 1976b). Galls containing eggs, larvae and puparia were sampled most recently from *A. dumosa* near Snow

Creek at 370-m elevation in the dry San Gorgonio River bed, Riverside Co., during February–April, 1993 and 1994, and from *A. eriocentra* at Mountain Pass during February–May, 1991–1995. Excised galls were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty-one and 19 larvae and 4 and 3 puparia dissected from galls on *A. dumosa* and *A. eriocentra*, respectively, were preserved in 70% EtOH for scanning electron microscopy (SEM). All other fully grown larvae and puparia from *A. eriocentra* were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM later were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia obtained from galls on *A. eriocentra* were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies and oviposition tests in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials as well as field-swept adults were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991) for direct observations, videorecording, and still-photography of their courtship and copulation behavior.

Plant names used in this paper follow Munz (1974); tephritid nomenclature and adult terminology follow Foote et al. (1993). Format used to describe the adults follows Blanc and Foote (1961). Morphological terminology and telegraphic format used to describe the immature stages follow Goeden and Headrick (1992), Headrick and Goeden (1990, 1993), Goeden et al. (1994a, b, 1995a, b), Goeden and Teerink (1996a, b, c), Headrick et al. (1995), and our other works cited therein. Means \pm SE are used throughout this paper. The holotypes, allotypes, and five individually reared paratypes of each sex of both new species have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Six additional, individually reared paratypes of each sex of both species also were deposited in the collection of the California Academy of Sciences (CAS). The holotype, allotype, and 22 paratypes used for measurements to describe *P. kristineae* originated from one collection in 1980 at the Palm Springs study site used by Silverman and Goeden (1980); the same numbers of types were used to describe *P. lisae* from one collection in 1981 at Mountain Pass. All remaining paratypes and voucher specimens not designated as paratypes and reared parasitoids of both tephritids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT.

RESULTS AND DISCUSSION

TAXONOMY

The new species from *A. dumosa* described below as *P. kristineae* is most similar to *P. stonei* Blanc and Foote, which it was first misidentified as (Silverman and Goeden 1980). However, adults of these two species are distinguished below mainly on the basis of their wing characters, instead of those often lacking in swept or preserved specimens, e.g., distribution patterns

of setae on the scutum, consistent with the philosophy embodied in the key to U.S. and Canadian species of *Procecidochares* in Foote et al. (1993). The new species from *A. eriocentra* described as *P. lisae* also is distinguished below primarily by wing characters. Accordingly, the following key couplets replacing couplets 1 and 5 in the key of Foote et al. (1993) enable one to distinguish these two new species:

- 1. Pterostigma lighter brown in basal fifth to half than in apical part; sometimes a second orbital bristle 1a
- Pterostigma evenly brown; 1 pair orbital bristles 2
- 1a. Two orbital bristles, the second pair very small and delicate; basal and discal bands separate. *flavipes* Aldrich
- One pair of orbital bristles; basal and discal bands usually connected 1b
- 1b. Gena with prominent dark brown spot at ventral margin of eye; discal band not extended posterior to vein $A_1 + CuA_2$ in male, usually crossing it in female, but fading towards posterior wing margin; basal and discal bands broadly connected in cells *c*, *sc*, *br*, and *bm* *lisae* Goeden, n. sp.
- Gena with ochereous to pale brown spot at ventral margin of eye; discal band extending distinctly to posterior wing margin in both sexes; basal and discal bands narrowly connected in cell *sc* or *br* *kristinae* Goeden, n. sp.

**Procecidochares kristinae Goeden,
new species**
(Figs. 1, 3–7)

Procecidochares stonei Blanc and Foote: Wasbauer 1972: 7 (in part, *Ambrosia dumosa* host record).

Procecidochares n. sp.: Goeden and Ricker 1976a: 49 (host record).—Silverman and Goeden 1980: 283–288 (host, gall description, California distribution, biology, behavior, seasonal history, parasitoids, predators, gall inquiline).—Foote et al. 1993: 318 (taxonomic status)

Female (Holotype).—*Head*: In profile 0.6 to 0.7 times as long as high, face and frons meeting at an angle of about 120°; parafacial 0.75 times as wide as third antennal segment; gena about 0.2 times as high as eye, which is 0.5 to 0.6 as wide as

high; frons ochereous brown to yellow or white, at vertex 1.4 to 1.6 times as wide as eye in lateral view, 1.2 to 1.3 times as wide as length from vertex to lunule; lunule half as high as its width between the antennae; face yellow to white, pollinose, concave, but raised medially and protruding slightly at middle of oral margin; antenna yellow, pollinose, third segment sometimes ochereous brown along anterior margin and apex, arista ochereous brown to black, lightest basally. Usually 3–4 frontal bristles (rarely 5 or 6), all black; one pair of black orbital bristles; black genal bristle slender, situated immediately below lower curvature of eye; all postoculars white.

Thorax: Pleuron mostly shining dark brown to black, especially the katepisternum, but with a very sparse pollinosity on anepisternum; katepisternal bristle black, most other pleural setae rather long and white; wing base and anepimeron densely silver pollinose over a dark brown to black ground-color; lateral third of mesonotum, including postpronotal lobe, shining dark brown to black; a wide, silvery pollinose stripe on a shiny black ground-color occupying median third of mesonotum from anterior margin nearly to scutoscutellar suture, slightly widened at transverse suture and invested with short, white, blunt setae (sometimes appearing pale yellow) as follows: scattered ± uniformly over median pollinose strip, except for anterior half of presutural part of scutum, where confined to center and margins of strip, also encircling the lateral third of presutural part of scutum including along the transverse suture, and trailing posteriolaterad and posteriomedial in separate rows 3 to 4 setae-wide, the outer row narrowing and crossing the scutoscutellar suture to end in a cluster of 5 to 12 setae at base of anterior scutellar bristle. One dorsocentral bristle situated about halfway between transverse suture and level of the postsutural supra-alar bristle, and located on margin of median pollinose area; cluster of 5 to 8 short, white setae anteriorad of base of postsutural supra-alar bristle.

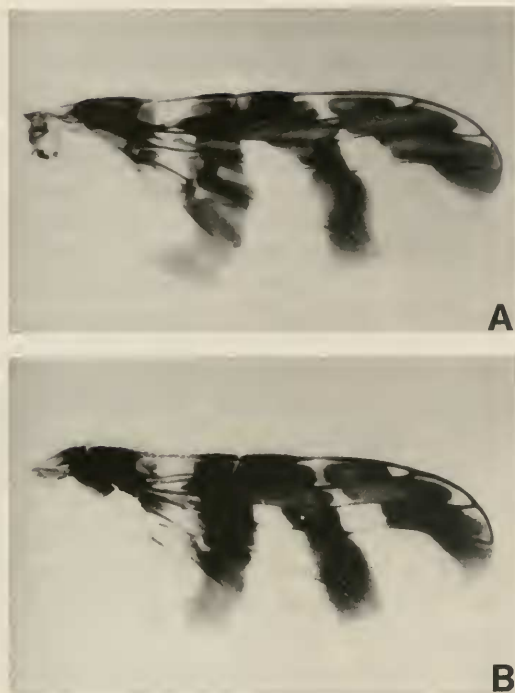


Fig. 1. Right wings of *Procacidochares kristineae*: (A) female; (B) male.

Scutellum shining dark brown to black, bulbous, two pairs scutellar bristles; postscutellum dark brown to black, pollinose. Haltere shaft ochereous yellow, slightly darker than knob. Femora of fore, mid, and hind legs dark brown but with yellow extremities, the remainder of legs yellow to ochereous yellow. Wing pattern as in Fig. 1A, B; pterostigma about 2.0 times as long as wide, lighter in basal fifth to third; basal and discal bands narrowly joined in cell br and/or sc, subapical and apical bands usually joined in cell(s) r_1 and/or r_{2+3} (Fig. 1A) or sometimes narrowly separated (Fig. 1B) and only joined by darkened portions of veins R_{2+3} and R_{4+5} ; distance between crossveins r-m and dm-cu measured along vein M about equal to length of r-m.

Abdomen: Dark brown to black, each tergum covered with white, flattened setae progressively increasing in length posteriorly. Oviscape shining dark brown to black, basal half slightly swollen, about half as

long as all terga, except the first, taken together.

Male (allotype).—*Head*: Like ♀, but parafacial 0.67 times as wide as third antennal segment; frons at vertex 1.1 to 1.3 times as wide as one eye, 1.1 to 1.4 times as wide as distance from vertex to lunule; lunule 0.5 to 0.7 times as high as its width at antennal base. *Thorax*: Like ♀. *Abdomen*: Like ♀, only external genitalia dark brown to black.

Variation.—Examination of *P. kristineae* specimens with mostly intact setation confirmed variation in numbers of frontal setae, noted for the genus to vary from two to five by Foote et al. (1993). The holotype and 19 ♀ paratypes (68%) of a total of 28 ♀ types examined had three pairs of frontal setae; one pair of these setae was white in two ♀, and one pair was reduced in length and thickness in another ♀. One ♀ had four pairs of frontal setae; another ♀ had five pairs. The frontal setae were not strictly paired in the remaining six ♀, as four ♀ had three and four frontal setae on different sides of their heads; and each of two ♀, four and five frontal setae located asymmetrically. The allotype and 32 ♂ paratypes (64%) of a total of 50 ♂ types examined had three pairs of frontal setae. Three ♂ (6%) had four pairs of frontal setae. Among the remaining 15 ♂, nine (18%) had three and four frontal setae on different sides of their heads, four ♂ (16%) each had three and five frontal setae, and one ♂ each had four and five or four and six frontal setae located asymmetrically.

Regarding the wings, the subapical and apical bands also showed variation. The holotype and 14 ♀ paratypes (48%) of a total of 31 ♀ types with intact wings had the subapical and apical bands broadly joined (Fig. 1A); 7 ♀ paratypes (23%) had the subapical and apical bands narrowly joined in at least one wing (in the other wing in 5 of these ♀, these bands were narrowly separated, Fig. 1B); and in the remaining 9 ♀ (29%), these bands were narrowly separated in both wings. The allotype and 25 ♂

types (49%) of a total of 51 ♂ paratypes with intact, fully formed wings had the subapical and apical bands broadly joined (Fig. 1A); 8 ♂ paratypes (16%) had these bands narrowly joined in at least one wing (in the other wing in 1 ♂, these bands were narrowly separated); and in the remaining 18 ♂ paratypes (35%), these bands were narrowly separated in both wings.

Diagnosis.—The two main morphological characters distinguishing the adults of *P. kristineae* are the pterostigma being lighter brown in the basal fifth to third than in the apical part (Fig. 1), in combination with one pair of orbital setae. All types of *P. kristineae* possessed these two characters. The former character is shared only with *P. flavipes* and *P. lisae* (see below); the latter character distinguishes *P. flavipes* which has two pairs of orbital setae (Foote et al. 1993). *Procecidochares kristineae* and *P. lisae* are distinguished below. In the partial key provided above, if the pterostigmal character is missed *P. kristineae* will run to *P. stonei*, the only other species with basal and discal bands connected. Most *P. kristineae* differ from *P. stonei* by having the subapical and apical bands broadly to narrowly joined.

Of 179 reared voucher specimens of *P. stonei* with fully formed wings in the research collection of RDG (Green et al. 1993), 14 (8%) had a pterostigma in at least one wing that was light basally, but usually this basal area was small and only partially extended posteriorad across the cell, nor were the subapical and apical bands in the wings of these 14 flies joined. Similarly, another 12 voucher specimens of *P. stonei* had at least one wing with the subapical and apical bands joined, but all of these flies had pterostigmas that were evenly brown. Additional biological and ecological characteristics that distinguish *P. kristineae* and *P. stonei* are discussed below.

Types.—Holotype, ♀; 8 km NE of Palm Springs, 250-m elevation, Riverside Co., California; 26.ii.1981; R. D. Goeden, coll.(hereafter, RDG, coll.); reared from ax-

illary bud gall on *A. dumosa* [at study site of Silverman and Goeden (1980)] (USNM); allotype, ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 12 ♂ and 24 ♀; same data as holotype (5 ♂ and 5 ♀ to USNM, 6 ♂ and 6 ♀ to CAS). 4 ♂ and 3 ♀; same location data as holotype; 10.ii.1971; RDG and D.W. Ricker, coll. (hereafter, RDG & DWR, coll.). 1 ♀; Twentynine Palms, San Bernardino Co.; 25.iii.1970; RDG & DWR, coll. 4 ♂ and 1 ♀; Llano, San Bernardino Co.; 30.iv.1970; RDG & DWR, coll. 6 ♂ and 1 ♀; Yucca Valley, San Bernardino Co.; 4.iii.1971; RDG & DWR, coll. 1 ♀; Borrego Springs, San Diego Co., 1.ii.1973; RDG & DWR, coll. 5 ♂ and 7 ♀; Valliceto Valley, S end of Smugglers Canyon at 442 m, San Diego Co.; 11.iii.1993; RDG and J.A. Teerink, coll. (hereafter, RDG & JAT, coll.). 5 ♂ and 4 ♀; Snow Creek at 370 m, Riverside Co.; 7.iv.1994; RDG & JAT, coll. 3 ♂ and 3 ♀; Ocotillo, Imperial Co., 2.ii.1995; RDG & JAT, coll. (Remaining 39 ♂ and 20 ♀ paratypes along with numerous swept and/or damaged-reared, voucher and nonvoucher specimens examined and identified are held in research collection of RDG).

Etymology.—*Procecidochares kristineae* is named for my younger daughter, Kristine Louise Gilbert (nee Goeden), mother of my two grandsons, Samuel Vanderpoel Gilbert V and Nikolaus Richard Gilbert.

***Procecidochares lisae* Goeden,
new species
(Figs. 2, 8–12)**

Procecidochares n. sp.: Goeden and Ricker (1976b): 927 (host record).

Female (holotype).—**Head:** In profile 0.5 to 0.6 times as long as high, face and frons meeting at an angle of about 120°; parafacial as wide as third antennal segment; gena with prominent, shiny, dark-brown spot from lower margin of eye to genal groove, gena 0.1 to 0.2 times as high as eye, which is 0.4 to 0.5 as wide as high; frons ochereous yellow to white, at vertex 1.3 to 1.7 times

as wide as eye in lateral view, 1.3 to 1.6 times as wide as length from vertex to lunule; lunule 0.4 to 0.6 times as high as its width between the antennae; face pale yellow to white, pollinose, concave, but raised medially; antenna mostly brown, pollinose, apex of second segment and sometimes posterior margin of third segment yellow, arista ochereous yellow to brown, lightest basally. Usually, 3–4 frontal bristles (rarely 2 or 5), all black; one pair of black orbital bristles; genal bristle black, arising behind brown part of genal margin, which is extension of brown spot (noted above) below genal groove; all postoculars white.

Thorax: Pleuron mostly shining dark brown to black, especially the katepisternum, but with a very sparse pollinosity on anepisternum; katepisternal bristle black, most other pleural setae rather long and white; wing base and anepimeron densely silver pollinose over a dark brown to black ground-color; lateral third of mesonotum, including postpronotal lobe, shining dark brown to black; a wide, silvery pollinose stripe on a shiny black ground-color occupying median third of mesonotum from anterior margin nearly to scutoscuteellar suture, slightly widened at transverse suture and invested with short, white, blunt setae (sometimes appearing pale yellow) as follows: scattered \pm uniformly over median pollinose strip, except for anterior half of presutural part of scutum, where confined to center and margins of strip, also encircling the lateral third of the presutural part of scutum including along the transverse suture, encircling the anterolateral two-thirds of the scutum, and trailing posteriolaterad and crossing the scutoscuteellar suture to end in a cluster of 8 to 18 setae at base of anterior scutellar bristle. One dorsocentral bristle situated just anterior to a line between the postsutural supra-alars and slightly laterad of the margin of median pollinose area. Scutellum shining dark brown to black, bulbous, two pairs scutellar bristles; postscutellum dark brown to black, pollinose. Haltere shaft ochereous yellow, slightly darker



Fig. 2. Right wings of *Procacidochares lisae*: (A) female; (B) male.

than knob. Femora of fore, mid, and hind legs dark brown but with ochereous yellow extremities, the remainder of legs yellow to ochereous yellow. Wing pattern as in Fig. 2A pterostigma about 2.0 times as long as wide, lighter in basal fifth to half; basal and discal bands broadly joined in cells *c*, *sc*, and *br*; discal band usually shortened, crossing cell *cua*₁ along and distal to vein *CuA*₂, and nearly or just touching vein *A*₁ + *CuA*₂ growing faint if extending into anal lobe; subapical and apical bands usually separated, or sometimes narrowly joined in cell(s) *r*₁ and/or *r*₂₊₃; distance between crossveins *r-m* and *dm-cu* measured along vein *M* about equal to length of *r-m*.

Abdomen: Dark brown to black, each tergum covered with white, flattened setae progressively increasing in length posteriorad. Oviscape shining dark brown to black, basal half slightly swollen, about half as long as all terga, except the first, taken together.

Male (allotype).—*Head*: Like ♀, but about 0.6 times as long as high, face and frons meeting at an angle of about 110°; parafacial 0.67 times as wide as third antennal segment; eye 0.5 to 0.6 times as wide as high; frons at vertex 1.1 to 1.5 times as wide as eye, 1.3 to 1.7 times as wide as length from vertex to lunule; lunule 0.5 to 0.7 times as high as its width at antennal base. *Thorax*: Like ♀, but discal band of wing rarely extending into anal lobe and usually ending before and not touching vein $A_1 + CuA_2$; subapical and apical bands usually separated, but sometimes narrowly or widely joined in cell(s) r_1 and/or r_{2+3} (Fig. 2B). *Abdomen*: Like ♀, only external genitalia dark brown to black.

Variation.—Examination of *P. lisae* specimens with mostly intact setation further confirmed variation in numbers of frontal setae for the genus (Foote et al. 1993). The holotype and 30 ♀ paratypes (50%) of a total of 62 ♀ types examined had three pairs of frontal setae. Six ♀ paratypes (13%) each had four pairs of frontal setae; another ♀ had five pairs. The frontal bristles were not paired in the remaining 22 ♀, as 19 ♀ had three and four frontal setae on different sides of their heads; two ♀ had two and three frontal setae located asymmetrically; and one ♀ had three and six frontal setae so located. The allotype and 25 ♂ paratypes (53%) of a total of 47 ♂ types examined had three pairs of frontal setae. Eight ♂ paratypes (13%) each had four pairs of frontal setae. Among the remaining 13 ♂ paratypes, nine (19%) had three and four frontal setae on different sides of their heads; two ♂ (4%) each had two and three frontal setae, and one ♂ each had three and five or four and five frontal setae located asymmetrically.

Regarding the wings, the relationship of the subapical and apical bands showed variation. The holotype and 48 ♀ paratypes (69%) of a total of 71 ♀ types with intact wings had the subapical and apical bands fully separated (Fig. 2A); 13 ♀ paratypes (18%) had the subapical and apical bands

narrowly separated; and in the remaining 9 ♀ (13%), these bands were narrowly or widely joined in cell r_1 in eight ♀ and one ♀, respectively. The allotype and 21 ♂ paratypes (45%) of a total of 49 ♂ types with intact, fully formed wings had the subapical and apical bands fully separated (Fig. 2B); 19 ♂ paratypes (39%) had these bands narrowly separated in at least one wing (in the other wing in four ♂, these bands were narrowly joined in cell r_1 or r_{2+3}); and in the remaining eight ♂ paratypes (16%), these bands were broadly joined in four ♂ or narrowly joined in four ♂ in cell r_1 or r_{2+3} .

In the holotype and 35 ♀ paratypes (51%) of the same 71 ♀ types with fully developed wings, the discal band extended across vein $A_1 + CuA_2$ into the anal lobe in both wings (Fig. 2A); in 27 ♀ paratypes (37%), this band ended at this vein in both wings; in two ♀ paratypes (3%) each wing showed a different one of these two characters. In only three (4%) of the remaining ♀ paratypes, the discal band ended before and did not reach vein $A_1 + CuA_2$. In the allotype and 39 ♂ paratypes (80%) of the same 49 ♂ types with intact, fully formed wings, the discal band ended before and did not touch vein $A_1 + CuA_2$ (Fig. 2B), or reached this vein in nine (18%) other ♂ paratypes, but crossed this vein into the anal lobe in only one ♂ paratype. These data, therefore, provide the first documented incidence of sexual dimorphism in the wing pattern of a species of *Procecidochares* (Foote et al. 1993); although, this dimorphism pales in comparison with wing pattern sexual dimorphism recently reported by us for certain species of *Aciurina* (Goeden and Teerink 1996a, b, c), or as long known for certain *Trupanea* spp. (Foote et al. 1993).

Diagnosis.—The incomplete discal band distinguishes *P. lisae* from all previously described species of *Procecidochares*. Two other characters distinguishing the adults of *P. kristineae* and *P. lisae* from other *Procecidochares* spp. are the pterostigma being lighter brown in the basal fifth to half than

in the apical part, in combination with one pair of orbital setae. These species can then be readily separated on the basis of their wing patterns and the color of the genal spot as described in the partial key provided above. The pterostigmal character is shared only by *P. flavipes*, *P. kristineae*, and *P. lisae*, with *P. flavipes* separated by its possession of two pairs of orbital setae. The basal and discal bands are joined only in the wings of *P. kristineae*, *P. lisae*, and *P. stonei*, with *P. lisae* readily distinguished by the broad anterior juncture of these bands and by the shortened discal bands.

Types.—Holotype, ♀; Mountain Pass, 1430-m elevation, NE San Bernardino Co., California; 30.iv.1981; RDG, coll.; reared from axillary bud gall on *A. eriocentra* (USNM); allotype, ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 17 ♂ and 17 ♀; same data as holotype (5 ♂ and 5 ♀ to USNM, 6 ♂ and 6 ♀ to CAS). 5 ♂ and 1 ♀, 2 ♂ and 2 ♀; same location data as holotype; 19.iv.1971, 26.vi.1971, respectively; RDG & DWR, coll. 5 ♂ and 3 ♀, 2 ♀, 10 ♂ and 11 ♀; same location data as holotype; 9.v.1991, 9.v.1992, 9.v.1993, respectively; RDG & JAT, coll. 8 ♂ and 15 ♀; Halloran Springs, NE San Bernardino Co.; 19.iv.1971; RDG & DWR, coll. 3 ♀; Halloran Springs, NE San Bernardino Co.; 29.iv.1981; RDG, coll. 1 ♀, 1 ♂ and 1 ♀; Hackberry Mountain, NE San Bernardino Co.; 22.ix.1970, 4.iii.1971, respectively; RDG & DWR, coll. 3 ♂ and 4 ♀; Granite Cove, NW San Bernardino Co., 25.v.1971; RDG & DWR, coll. (Remaining 36 ♂ and 50 ♀ paratypes along with numerous swept and/or damage-reared, voucher and non-voucher specimens examined and identified are held in research collection of RDG).

Etymology.—*Procecidochares lisae* is named for my older daughter, Lisa Marie Goeden, a unique woman of many accomplishments.

IMMATURE STAGES

Procecidochares kristineae.—Egg: Eggs of *P. kristineae* (Fig. 3A, B), were de-



Fig. 3. Egg of *Procecidochares kristineae* (A) habitus; (B) anterior end, aeropyles.

scribed by Silverman and Goeden (1980). Chorion smooth (Fig. 3A); pedicel with few aeropyles (Fig. 3B).

Third instar: Superficially smooth, elongate cylindrical, tapering anteriorly, lacking minute acanthae (Fig. 4A); gnathocephalon conical, broad dorsally, smooth with few rugose pads (Fig. 4B); paired dorsal sensory organs dorsomedial of anterior sensory lobes, consisting of dome-shaped papilla (Fig. 4B-1, 4C-1); anterior sensory lobes bear terminal sensory organ (Fig. 4C-2), pit sensory organ (Fig. 4C-3), lateral sensory organ (Fig. 4C-4), and supralateral sensory organ (Fig. 4C-5); stomal sense organs ventrad of anterior sensory lobe (Fig. 4B-2); lateral sensillum ventrolaterad of stomal sense organs (Fig. 4B-3); mouth hooks tridentate, teeth conical, stout (Fig. 4B-4); median oral lobe fleshy, tapering anteriorly, attached to labial lobe (Fig. 4B-5); labial lobe with two pore sensilla; ventro-

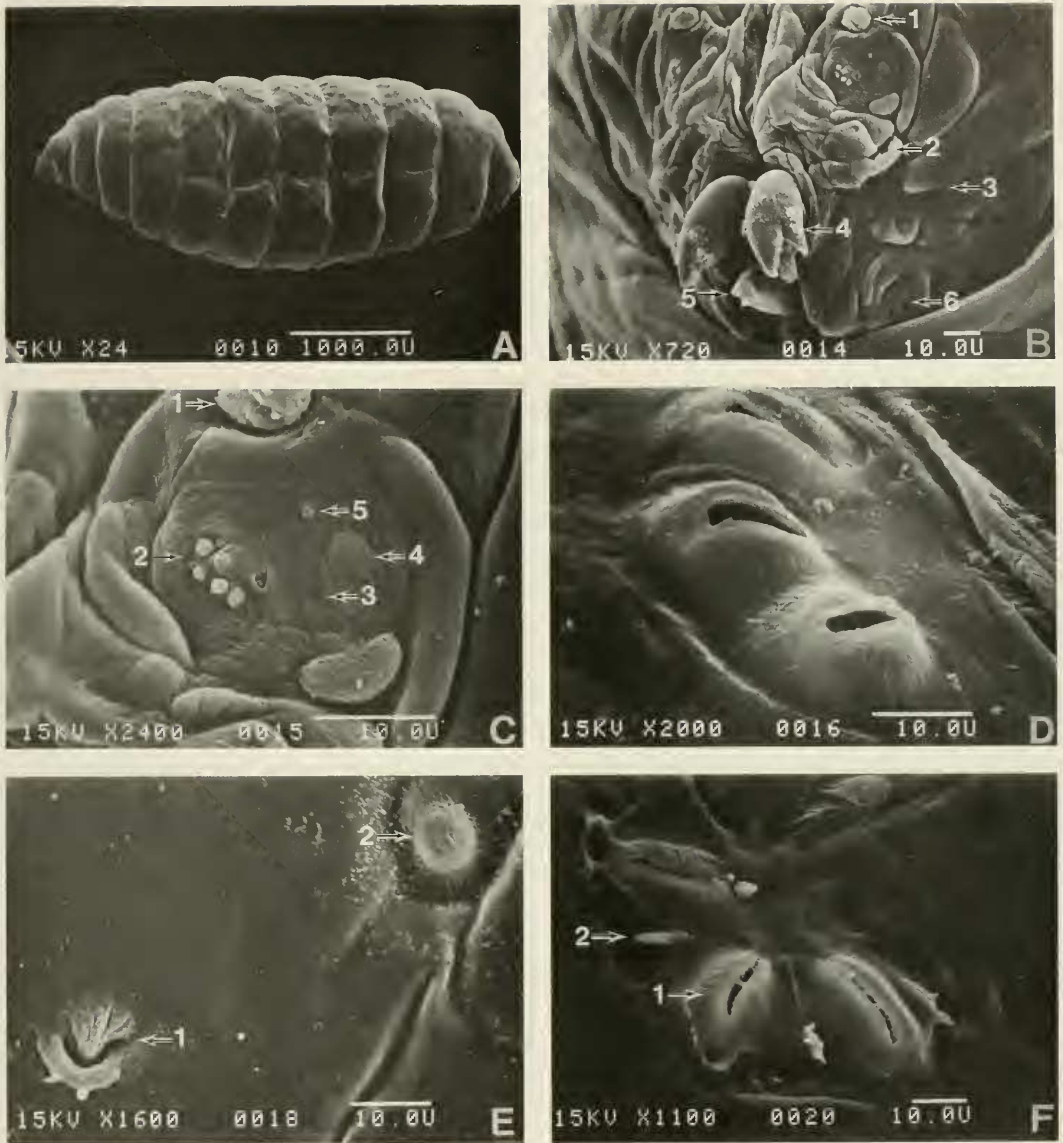


Fig. 4. Third instar of *Procecidochares kristineae*: (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—stomal sense organ, 3—lateral sensillum, 4—mouth hooks, 5—median oral lobe, 6—ventrolateral sensillum; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) anterior thoracic spiracles; (E) second abdominal lateral spiracular complex, 1—spiracle, 2—verruciform sensillum; (F) posterior spiracular plate, 1—rima, 2—interspiracular process.

lateral sensillum ventrolaterad of mouth lumen (Fig. 4B-6); prothorax smooth, verruciform sensilla circumscribe dorsal half of anterior margin, anterior thoracic spiracles on posterior margin consist of three ovoid papillae (Fig. 4D); meso- and

metathoracic lateral spiracular complexes consist of an open spiracle; abdominal lateral spiracular complex consist of an open spiracle (Fig. 4E-1) and a single verruciform sensillum (Fig. 4E-2); caudal segment bears posterior spiracular plates (Fig. 4F);

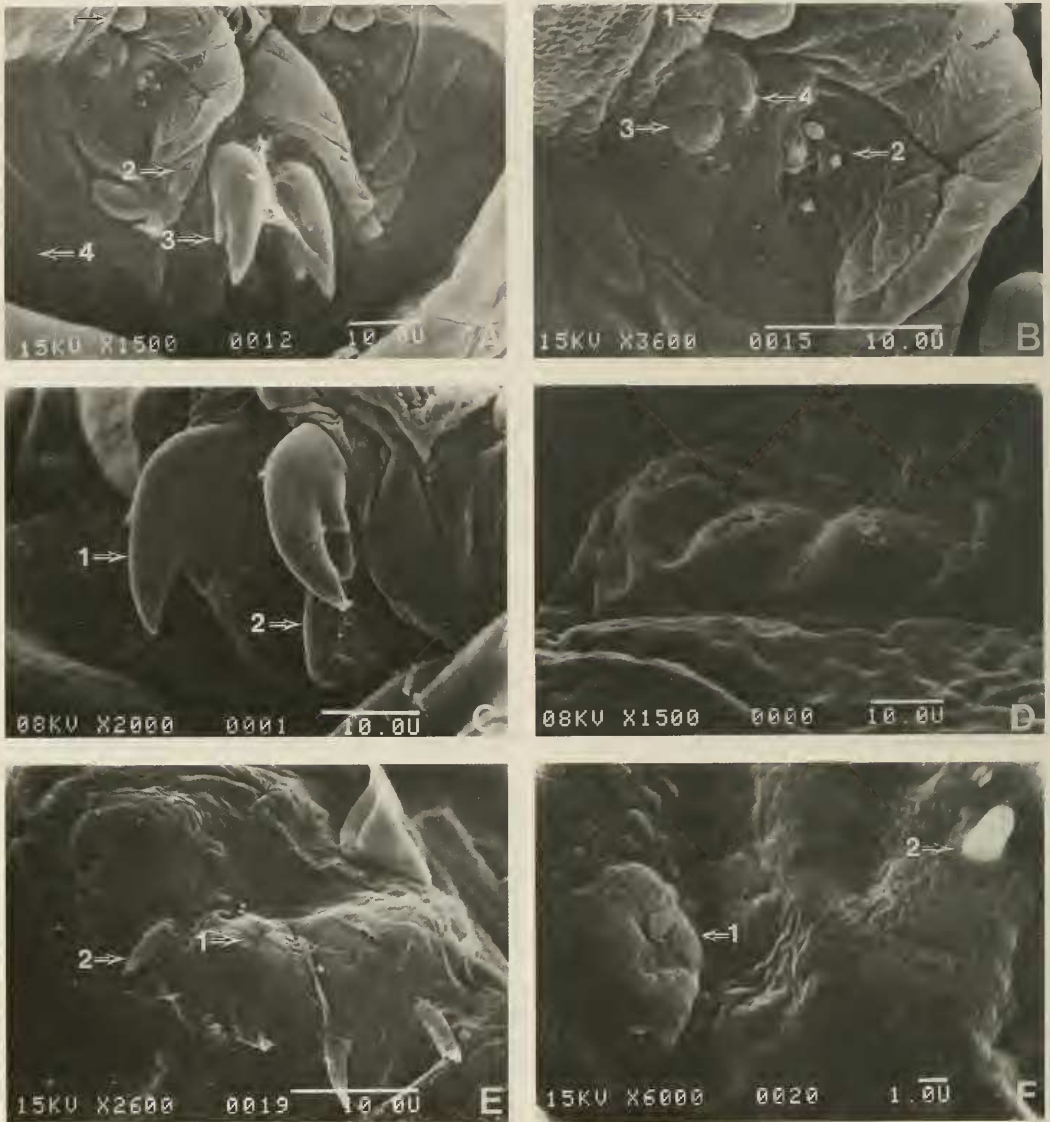


Fig. 5. Second instar of *Procecidochares kristineae*: (A) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—stomal sense organ, 3—mouth hooks, 4—ventrolateral sensillum; (B) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—supralateral sensory organ; (C) gnathocephalon, anteriolateral view, 1—mouth hooks, 2—median oral lobe; (D) anterior thoracic spiracles; (E) posterior spiracular plates, 1—rima, 2—interspiracular process; (F) compound sensillum, 1—verruciform sensillum, 2—stelex sensillum.

posterior spiracular plates with three ovoid rimae, ca. 0.024 mm in length (Fig. 4F-1), and four spiniform interspiracular processes, longest measuring 0.01 mm in length (Fig. 4F-2); compound sensilla ventrad of posterior spiracular plates consist of a verruciform sensillum and a stelex sensillum.

Second instar: Superficially smooth, barrel-shaped, rounded anteriorly and posteriorly; gnathocephalon conical, smooth with few rugose pads (Fig. 5A); paired dorsal sensory organs consist of a dome-shaped papilla (Fig. 5A-1, B-1); anterior sensory lobe bears terminal sensory organ (Fig.

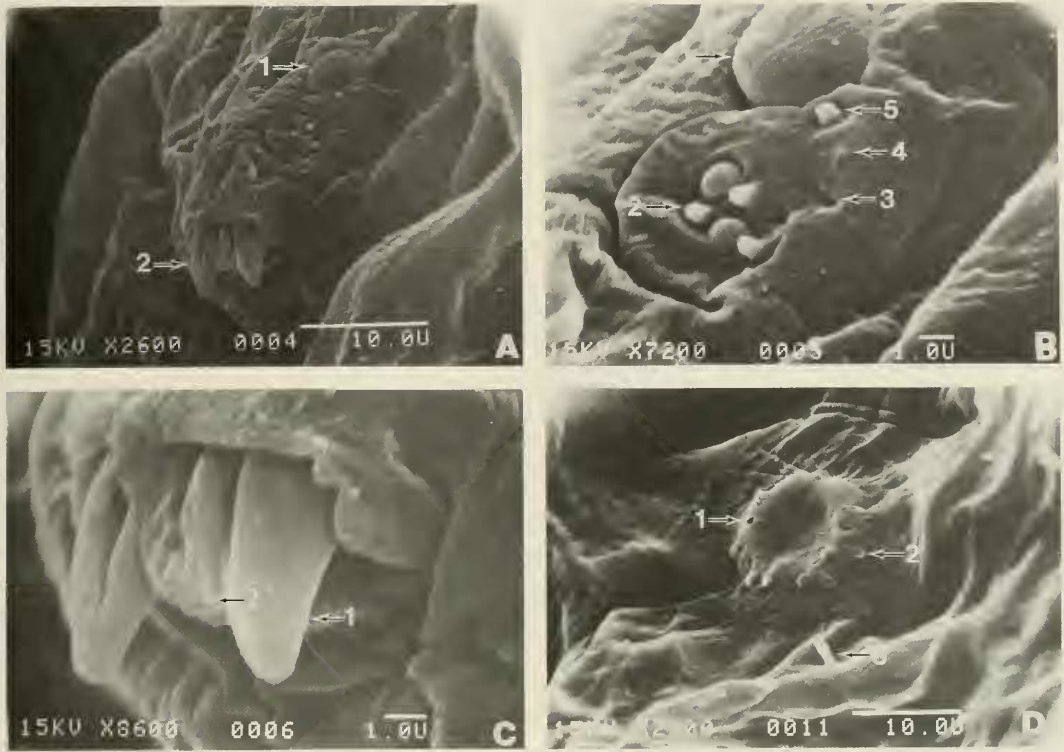


Fig. 6. First instar of *Procecidiochares kristineae*: (A) gnathocephalon, anteriolateral view, 1—dorsal sensory organ, 2—mouth hooks; (B) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (C) gnathocephalon, anteriolateral view, 1—mouth hooks, 2—median oral lobe; (D) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process, 3—stelex sensillum.

5B-2), pit sensory organ, lateral sensory organ (Fig. 5B-3), and supralateral sensory organ (Fig. 5B-4); stomal sense organ ventrad of anterior sensory lobe (Fig. 5A-2); mouth hooks tridentate, teeth conical, apical tooth longest (Fig. 5A-3, C-1); median oral lobe laterally flattened, rounded apically (Fig. 5C-2); ventrolateral sensillum ventrolaterad of mouth lumen (Fig. 5A-4); anterior thoracic spiracles on posterior margin of prothorax, consist of three ovoid papillae (Fig. 5D); lateral spiracular complex not observed; caudal segment bears posterior spiracular plates (Fig. 5E); posterior spiracular plates with three ovoid rimae, ca. 0.009 mm in length (Fig. 5E-1) and four spini-form interspiracular processes, longest measuring 0.005 mm (Fig. 5E-2); compound sensilla ventrad of posterior spiracular

plates, consist of a verruciform sensillum (Fig. 5F-1), and a stelex sensillum (Fig. 5F-2).

First instar: Superficially smooth, barrel-shaped, rounded anteriorly and posteriorly, minute acanthae circumscribe segmental lines; gnathocephalon conical, smooth, lacking rugose pads (Fig. 6A); dorsal sensory organ consists of a dome-shaped papilla (Fig. 6A-1, B-1); anterior sensory lobes bear terminal sensory organ (Fig. 6B-2), pit sensory organ (Fig. 6B-3), lateral sensory organ (Fig. 6B-4), and supralateral sensory organ (Fig. 6B-5); stomal sense organs indistinct; mouth hooks bidentate, apical tooth with v-shaped frontal groove along entire length (Fig. 6A-2, 6C-1); median oral lobe rounded apically (Fig. 6C-2); anterior thoracic spiracles absent; lateral

spiracular complexes not observed; caudal segment bears posterior spiracular plates (Fig. 6D); posterior spiracular plates with two ovoid rimae, ca. 0.002 mm (Fig. 6D-1), and four ovoid interspiracular processes, longest measuring 0.001 mm (Fig. 6D-2); stelix sensillum ventrad of posterior spiracular plates (Fig. 6D-3).

Puparium: Superficially smooth, elongate-ellipsoidal (Fig. 7A); anterior end bears invagination scar (Fig. 7B-1), and anterior thoracic spiracles (Fig. 7B-2); caudal segment bears posterior spiracular plates (Fig. 7C); posterior spiracular plates with three ovoid rimae, ca. 0.03 mm in length (Fig. 7C-1), and four spiniform interspiracular processes, longest measuring 0.01 mm (Fig. 7C-2). Measurements of *P. kristineae* puparia were provided by Silverman and Goeden (1980).

***Procecidochares lisae*.**—Egg: Fifty ova of *P. lisae* were white, opaque, smooth; with an elongate-ellipsoidal body, 0.57 ± 0.005 (range, 0.52–0.64) mm long, 0.17 ± 0.002 (range, 0.16–0.20) mm wide, smoothly rounded at tapered posterior end; and with a short, peg-like anterior pedicel, 0.02 mm long by 0.03 wide.

Third instar: Superficially smooth, elongate cylindrical, tapering anteriorly, lacking minute acanthae (Fig. 8A); gnathocephalon conical, broad dorsally, smooth with few rugose pads (Fig. 8B); paired dorsal sensory organs dorsomedial of anterior sensory lobes, consisting of dome-shaped papilla (Fig. 8B-1); anterior sensory lobes bear terminal sensory organ (Fig. 8B-2), pit sensory organ (Fig. 8B-3), lateral sensory organ (Fig. 8B-4), and supralateral sensory organ (Fig. 8B-5); stomal sense organs ventrad of anterior sensory lobe; lateral sensillum ventrolaterad of stomal sense organs (Fig. 8B-6); mouth hooks tridentate, apical tooth longest (Fig. 8C-1); median oral lobe fleshy, laterally flattened, tapering anteriorly, (Fig. 8C-2); ventrolateral sensillum ventrolaterad of mouth lumen (Fig. 8C-3); prothorax smooth, verruciform sensilla circumscribe dorsal half of anterior margin; ante-

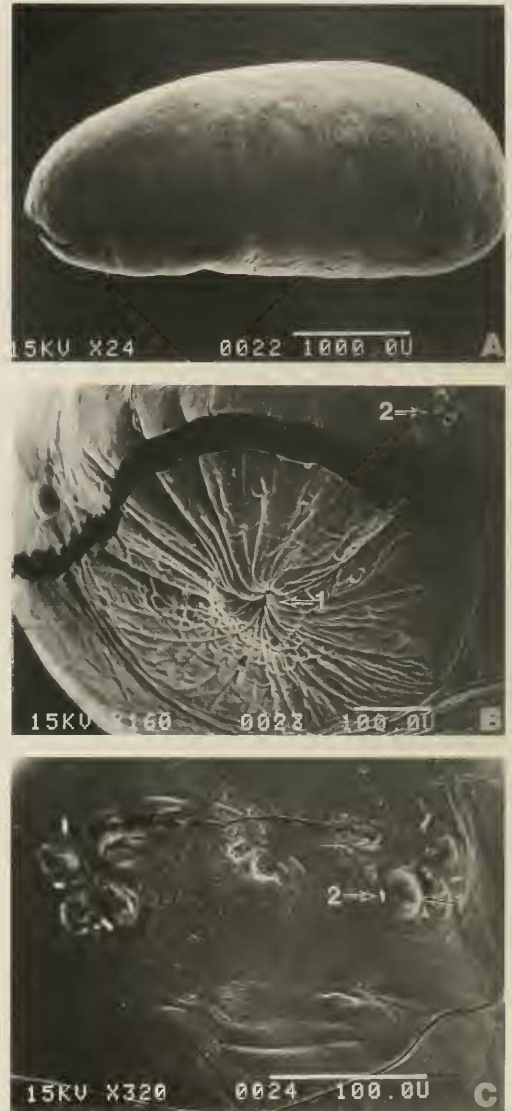


Fig. 7. Puparium of *Procecidochares kristineae*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracles; (C) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process.

rior thoracic spiracles consist of three ovoid papillae (Fig. 8D); meso- and metathoracic lateral spiracular complexes consist of an open spiracle; abdominal lateral spiracular complex consist of an open spiracle (Fig. 8E-1) and a single verruciform sensillum (Fig. 8E-2); caudal segment bears posterior

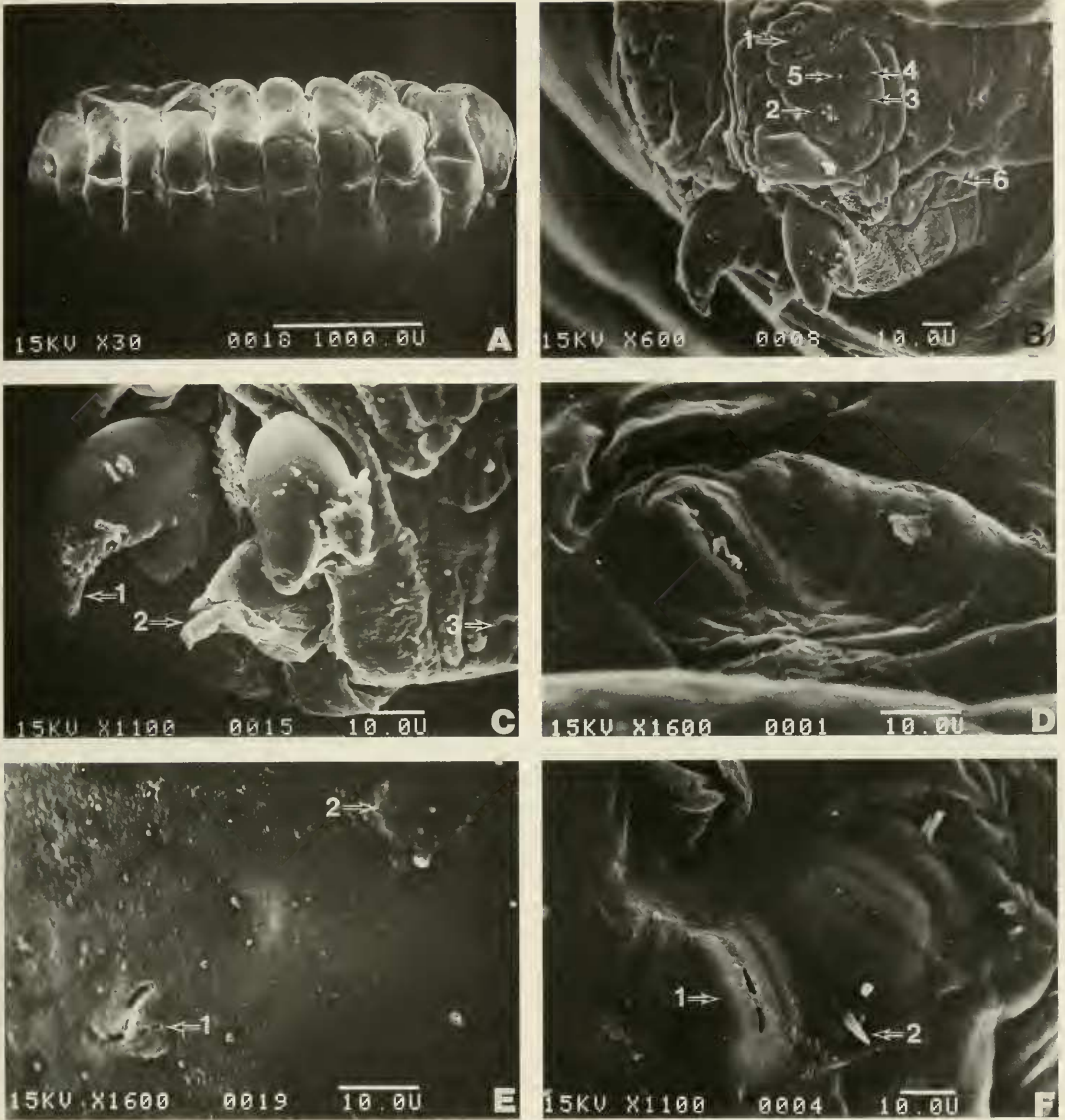


Fig. 8. Third instar of *Procecidochares lisae*: (A) habitus, anterior to left; (B) gnathocephalon, anteriolateral view, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—lateral sensillum; (C) gnathocephalon, anterior view, 1—mouth hooks, 2—median oral lobe, 3—ventrolateral sensillum; (D) anterior thoracic spiracles; (E) first abdominal lateral spiracular complex, 1—spiracle, 2—verruciform sensillum; (F) posterior spiracular plate, 1—rima, 2—interspiracular process.

spiracular plates; posterior spiracular plates with three ovoid rimae, ca. 0.025 mm in length (Fig. 8F-1), and four spiniform interspiracular processes, longest measuring 0.01 mm in length (Fig. 8F-2); compound sensilla ventrad of posterior spiracular plates consist of two verruciform sensilla.

Second instar: Superficially smooth, cylindrical, rounded anteriorly and posteriorly; gnathocephalon conical, smooth with few rugose pads; paired dorsal sensory organs consist of a dome-shaped papilla (Fig. 9A-1); anterior sensory lobe bear terminal sensory organ (Fig. 9A-2), pit sensory or-

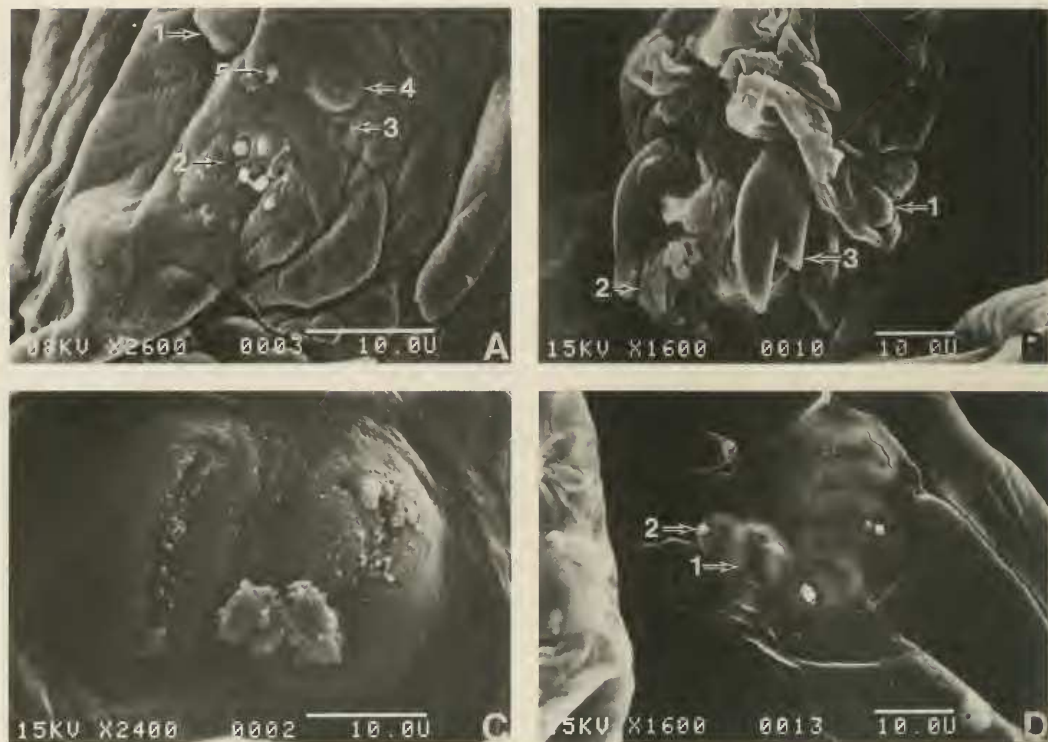


Fig. 9. Second instar of *Procecidochares lisae*: (A) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (B) gnathocephalon, anteriolateral view, 1—stomal sense organ, 2—median oral lobe, 3—mouth hooks; (C) anterior thoracic spiracles; (D) caudal segment, posterior spiracular plates, 1—rima, 2—interspiracular process.

gan (Fig. 9A-3), lateral sensory organ (Fig. 9A-4), and supralateral sensory organ (Fig. 9A-5); stomal sense organ ventrad of anterior sensory lobe (Fig. 9B-1); mouth hooks tridentate, teeth conical (Fig. 9B-3); median oral lobe fleshy, laterally flattened (Fig. 9B-2); anterior thoracic spiracles on posterior margin of prothorax, consist of two-three ovoid papillae (Fig. 9C); lateral spiracular complex not observed; caudal segment bears posterior spiracular plates; posterior spiracular plates with three ovoid rimae, ca. 0.009 mm in length (Fig. 9D-1) and four spiniform interspiracular processes, longest measuring 0.004 mm (Fig. 9D-2); compound sensilla ventrad of posterior spiracular plates were obscured in prepared specimens.

First instar: Superficially smooth, cylindrical, tapering anteriorly, rounded posteri-

orly, minute acanthae circumscribe segmental lines (Fig. 10A); gnathocephalon conical, smooth, lacking rugose pads (Fig. 10B); dorsal sensory organs large, dome-shaped (Fig. 10B-1, C-1); anterior sensory lobes bear terminal sensory organ (Fig. 10C-2), pit sensory organ (Fig. 10C-3), lateral sensory organ (Fig. 10C-4), and supralateral sensory organ (Fig. 10C-5); stomal sense organs indistinct; mouth hooks bidentate, apical tooth with v-shaped frontal groove along midline (Fig. 10B-2, D-1); ventrolateral sensillum ventrolaterad of mouth lumen (Fig. 10B-3, D-2); anterior thoracic spiracles absent; lateral spiracular complexes not observed; caudal segment bears posterior spiracular plates (Fig. 10E-1); posterior spiracular plates with two ovoid rimae, ca. 0.002 mm in length (Fig. 10F-1), and four, very reduced spiniform

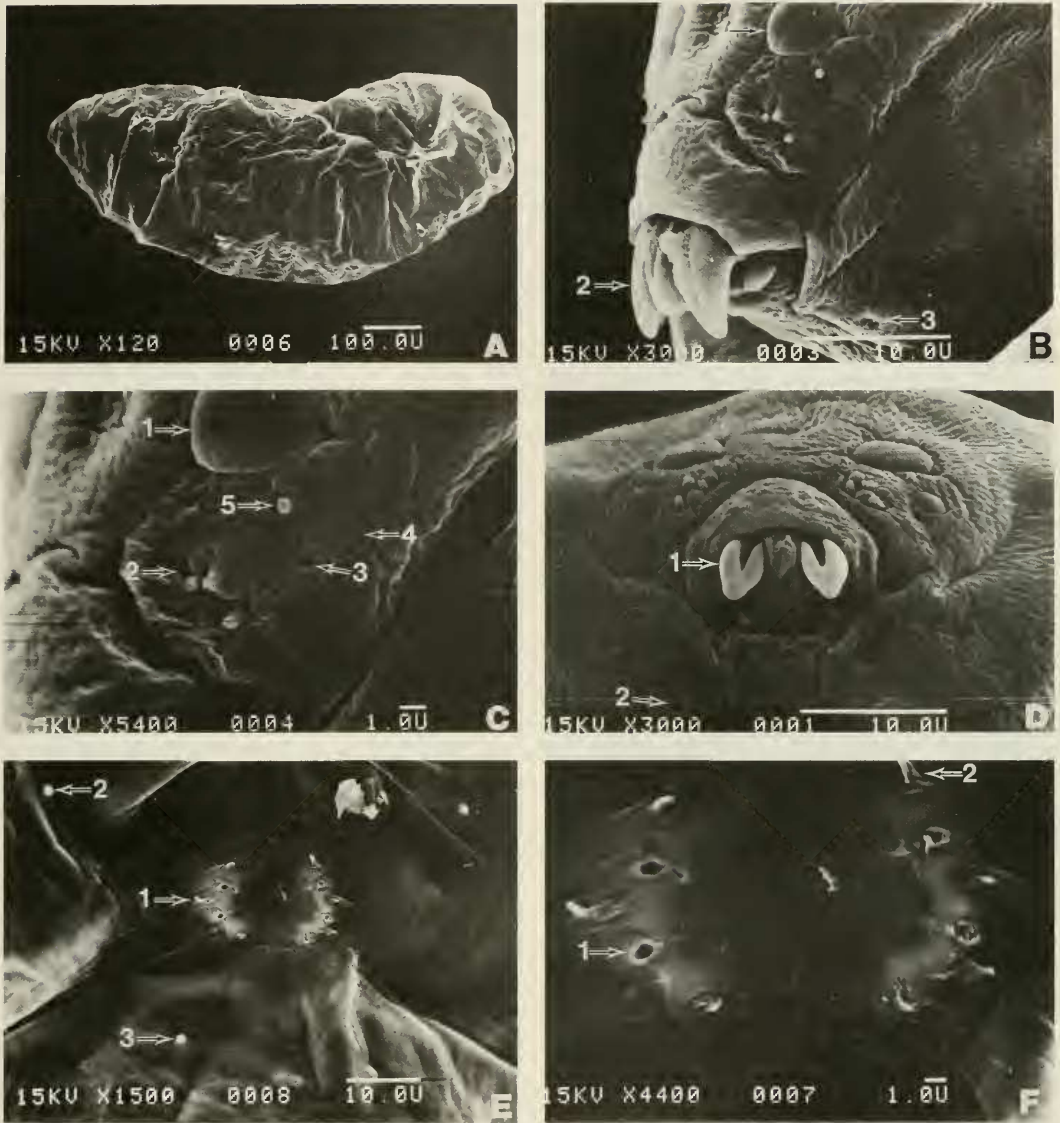


Fig. 10. First instar of *Procecidochares lisae*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1—dorsal sensory organ, 2—mouth hooks, 3—ventrolateral sensillum; (C) gnathocephalon, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ; (D) gnathocephalon, ventral view, 1—mouth hooks, 2—ventrolateral sensillum; (E) caudal segment, 1—posterior spiracular plates, 2—verruciform sensillum, 3—compound sensillum, verruciform sensillum; (F) posterior spiracular plates, 1—rima, 2—interspiracular process.

interspiracular processes, longest measuring 0.001 mm (Fig. 10F-2); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 10E-2); compound sensilla ventrad of posterior spiracular plates consist of two verruciform sensilla (Fig. 10E-3).

Puparium: Superficially smooth, elongate-ellipsoidal (Fig. 11A); anterior end bears invagination scar (Fig. 11B-1), and anterior thoracic spiracles (Fig. 11B-2); caudal segment bears posterior spiracular plates, each with three ovoid rimae, ca. 0.04

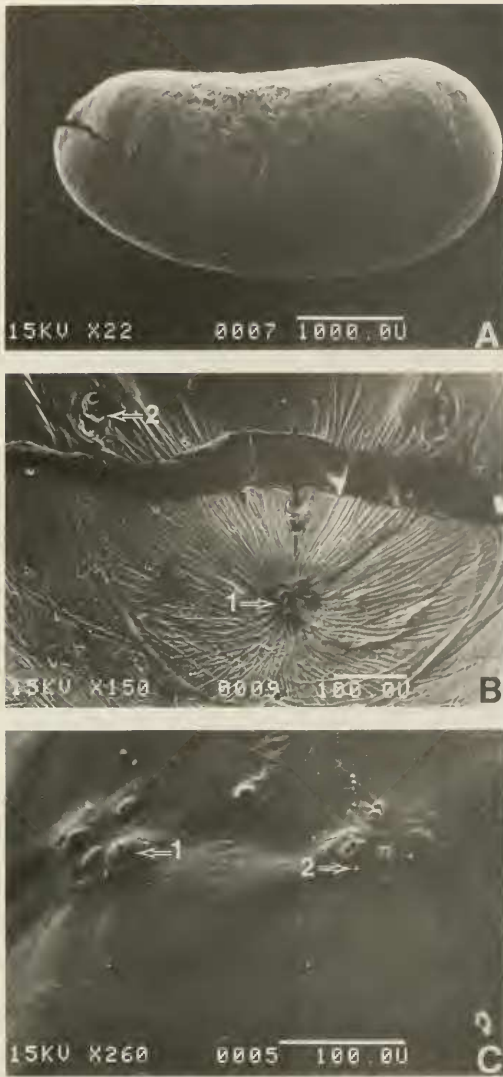


Fig. 11. Puparium of *Procecidochores lisae*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—rima, 2—interspiracular process.

mm in length (Fig. 11C-1), and four thorn-like interspiracular processes, longest measuring 0.007 mm (Fig. 11C-2). Fifty-six puparia averaged 4.01 ± 0.05 (range, 3.24-4.60) mm in length; 1.83 ± 0.03 (range, 1.40-2.35) mm in width.

Procecidochores kristineae and *P. lisae* larvae are morphologically very similar. The only difference noted was the com-

pound sensilla ventrad of the posterior spiracular plates; in *P. kristineae* there was a verruciform sensillum and a stelex sensillum, but both sensilla in *P. lisae* were verruciform. Thus, morphological differentiation between these two, possibly sibling species on separate, closely related hosts is minimal between their larvae, but distinctive between their adults. Similar morphological differences between larvae and adults of two sympatric, nongallicolous, also probably sibling species, *Trupanea nigricornis* and *T. bisetosa* recently was reported (Knio et al. 1996).

In turn, *Procecidochores kristineae* and *P. lisae* are very similar to *P. stonei* (Green et al. 1993). The noticeable difference between *P. stonei* and these two species in the third instar larva is that in the lateral spiracular complex, the verruciform sensillum is anteriorad of the spiracle in *P. stonei* not posteriorad. In the first instar of *P. stonei*, the mouth hooks are not grooved dorsally and the interspiracular processes are multi branched and blade-like (Green et al. 1993), not ovoid or spiniform and unbranched as in *P. kristineae* and *P. lisae*, respectively. *Procecidochores kristineae* and *P. lisae* are the first species of Tephritidae described with a v-shaped frontal groove in the apical tooth (Goeden and Headrick 1992; Goeden and Teerink 1996a, b, c; Goeden et al. 1994b; Green et al. 1993; Headrick and Goeden 1990; Headrick et al. 1995; Knio et al. 1996). The nongallicolous, flower head infesting species *P. flavipes* differs from all three of the above gall-forming species in having thoracic segments covered with small, polygonal rugose pads and the ventral intersegmental areas and dorsum of the caudal segment bearing minute acanthae (Goeden et al. 1994).

DISTRIBUTION AND HOSTS

Both *Procecidochores kristineae* and *P. lisae* are true monophages, each forming galls only on its sole host-plant species, *Ambrosia dumosa* and *A. eriocentra*, respectively. *Procecidochores kristineae* is

widely associated with *A. dumosa* in the Colorado and Mojave deserts of southern California (Goeden and Ricker 1976a, Silverman and Goeden 1980). Accordingly, the geographic distribution of *P. kristineae* may coincide wholly or partly with that of *A. dumosa* in southern Nevada, southwestern Utah, and western and southwestern Arizona (Benson and Darrow 1981), and southward into the Sonoran Desert of Baja California and Sonora, Mexico (Shreve and Wiggins 1964). The distributions of *P. lisae* and *A. eriocentra* in southern California are restricted to a small part of the northeastern Mojave Desert (Goeden and Ricker 1976b), but probably coincides wholly or partly with the wider distribution of this native ragweed in southern Nevada, southwestern Utah, and northwestern and central Arizona (Benson and Darrow 1981).

Estimating tephritid distribution from host-plant distribution is problematic because some gall-forming tephritid flies are known to be less widely distributed than their hosts, e.g., *A. bigeloviae* (Cockerell) and *A. trixa* Curran are widely allopatric, sympatric, or absent on *Chrysothamnus nauseosus* (Pallas) Britton in different parts of Utah, Arizona, New Mexico, and Colorado (Dodson and George 1986). Similarly, *A. trixa*, but apparently not *A. bigeloviae*, occurs in California on *C. nauseosus* which is a widespread plant species in southern California (D. H. Headrick, RDG, and JAT, unpublished data).

BIOLOGY

The biology of *P. kristineae* was described in considerable detail by Silverman and Goeden (1980). The following account largely concerns *P. lisae*, which then serves as a basis for comparison with *P. kristineae* and two other taxonomically-close *Procecidochares* spp. studied previously in southern California, *P. stonei* (Green et al. 1993) and *P. flavipes* (Goeden et al. 1994a).

Egg.—Most eggs are inserted singly and basally in axillary buds of the current season's branch growth. Some buds held two

or rarely three eggs, presumably oviposited by different females, judging by the slightly different degrees of development of two or three first instars found associated with single buds in field-collected branch samples (see below). Two eggs of *P. kristineae* per axillary bud also were reported as rare by Silverman and Goeden (1980). Adjacent axillary buds of infested branches bore eggs probably deposited in sequence by individual females as they moved in sequence to the next more-proximal axils, as described for *P. kristineae* (Silverman and Goeden 1980).

Larva.—Eggs hatch about a week after their deposition (Goeden and Silverman 1980, Green et al. 1993), but then the first instar larvae persist as the longest-lived stage in the life cycle of *P. lisae* within tiny open cavities of incipient galls (Fig. 12A). Single, aestivating first instars were found overwintering in ovoidal cavities 0.74 ± 0.03 (range, 0.54–0.93) mm long by 0.54 ± 0.02 (range 0.37–0.74) mm wide formed within, beneath, or immediately laterad of 26 axillary buds. Four pairs each of these first instars were associated with single axillary buds, and three first instars with another bud, documenting again multiple ovipositions in single buds. Each of these larvae continued to develop separately, as all galls examined of *P. lisae*, like *P. kristineae* (Silverman and Goeden 1980), contained only one larva in each. Thus, sometimes two or rarely three unilocular galls of *P. lisae* arose at the same axil; although, only one gall per axil was usual for both *P. kristineae* and *P. lisae* (Silverman and Goeden 1980). However, larvae of *P. stonei* develop gregariously in unilocular galls (Green et al. 1993).

The aforementioned 26 galls were sampled on 7.ii.1995, so that not only were these aestivating first instars the overwintering stage of *P. lisae*, but also the stage within which this species had persisted for 6 or 7 months since the previous April or May, when their parent adults emerged, mated, and oviposited. Both *P. kristineae*

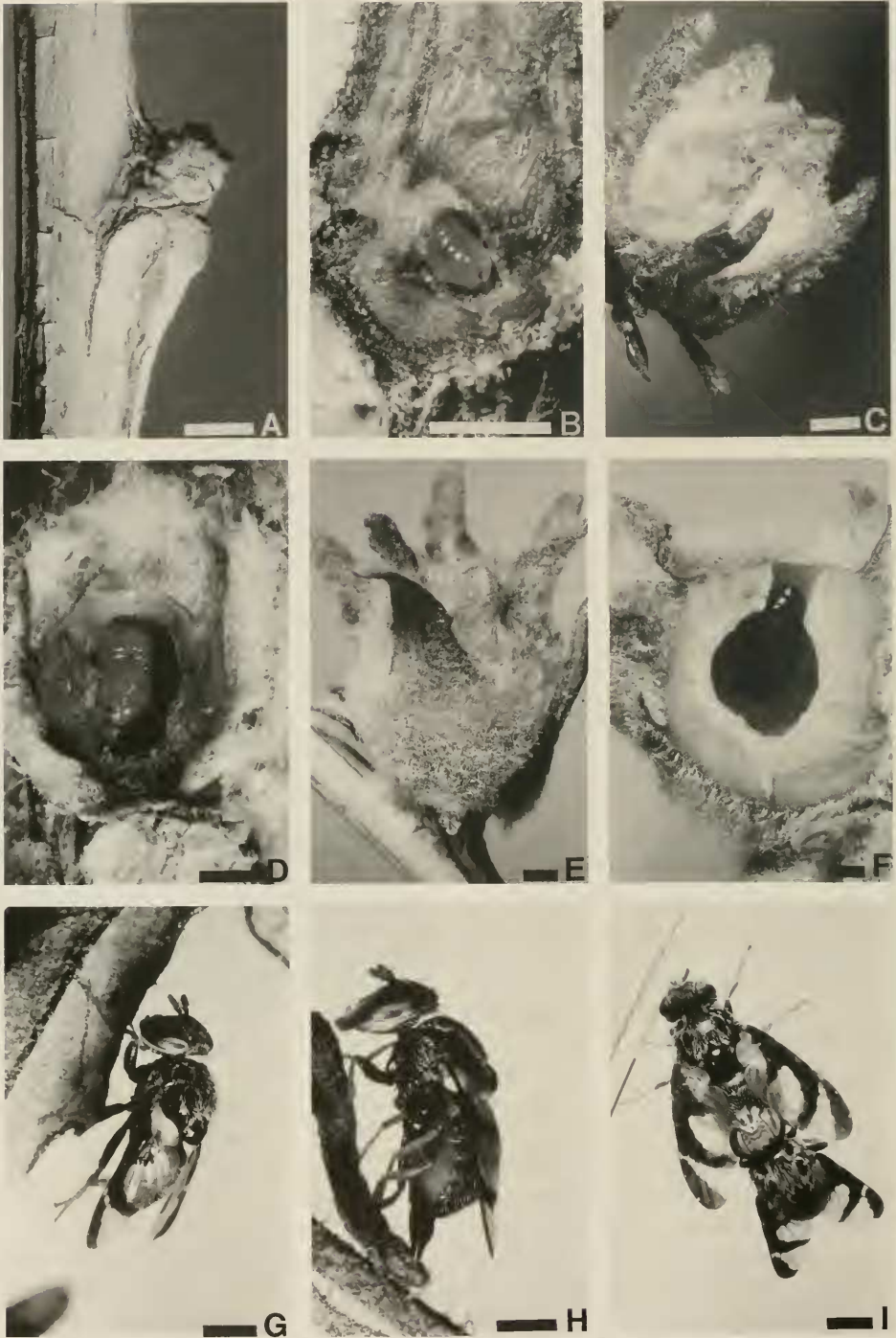


Fig. 12. Life stages of *Prociedochoares lisae* on *Ambrosia eriocentra*: (A) axillary bud gall containing aestivating first instar, (B) sagittal section of preceding axillary bud gall, (C) axillary bud gall containing second instar, (D) sagittal section of gall containing second instar, (E) full-size gall, (F) sagittal section through full-size gall containing a puparium, and showing exit channel excavated by late third instar, (G) lateral view of male, (H) lateral view of gravid female, (I) mating pair, dorsal view. Lines = 1 mm.

and *P. stonei* also overwinter as first instars in incipient galls (Silverman and Goeden 1980, Green et al. 1993). The tiny, overwintering galls of *P. lisae* were undetectable in the field (Fig. 12A, B); although those of *P. kristineae* were readily discerned (Silverman and Goeden 1980). The former galls caused only a slight axillary swelling along the leafless branches of dormant *A. eriocentra*, unlike overwintering galls of *P. kristineae* on *A. dumosa* which incorporated juvenile leaves (Silverman and Goeden 1980). The axils on branches where incipient galls of *P. lisae* were borne averaged 3.04 ± 0.05 (range, 2.5–3.6) mm in diameter ($n = 21$) and were located an average of 15.8 ± 1.1 (range, 6–24.5) cm from branch apex.

Following substantial late-winter/early-spring rainfall, host plants, galls, and larvae of *P. lisae* concurrently resume growth as also reported for *P. kristineae* (Silverman and Goeden 1980) and *P. stonei* (Green et al. 1993). Twenty-five galls of *P. lisae* containing second instars (Fig. 12C, D) averaged 5.72 ± 0.35 (range, 2.41–11.40) mm in length; 5.44 ± 0.34 (range, 2.28–11.40) mm in width. These spheroidal galls (Fig. 12C) contained single, ovoidal to spheroidal cavities (Fig. 12D) that averaged 2.53 ± 0.21 (range, 1.14–5.70) mm in length and 1.97 ± 0.16 (range, 0.57–4.56) mm in width. The gall walls averaged 1.12 ± 0.10 (range, 0.42–2.85) mm in thickness.

The larvae of *P. lisae* quickly grew and molted into the third and last larval instar within mostly spheroidal galls (Fig. 12E, F), 21 of which averaged 8.0 ± 0.4 (range, 4.3–11) mm in length and 7.1 ± 0.3 (range, 4.2–10) mm in width. The central ovoidal or spheroidal cavities were enlarged by larval feeding to an average of 4.1 ± 0.2 (range, 1.42–5.13) mm in length and 3.17 ± 0.18 (range, 1.42–5.13) mm in width. The lateral wall thickness averaged 1.18 ± 0.04 (range, 0.57–2.15) mm. Prior to pupariation, the third instar chews an exit tunnel through the gall wall (Fig. 12F) ending in a thin, circular to oval, epidermal win-

dow 1.4 ± 0.04 (range, 1.2–1.7) mm ($n = 13$) in diameter.

Pupa.—Fifty-six galls containing puparia (Fig. 12F), and thus of maximum size and final subspheroidal shape, averaged 10.2 ± 0.4 (range, 3.9–16) mm in length; 8.9 ± 0.3 (range, 3.5–16) mm in width. The ovoidal to spheroidal cavities of these mature galls averaged 4.8 ± 0.2 (range, 3.1–3.4) mm in length; 4.0 ± 0.1 (range, 2.6–6.2) mm in width. The lateral walls of these galls averaged 1.58 ± 0.06 (range, 0.51–2.58) mm in thickness.

Adult.—The adults (Fig. 12G, H) of *P. lisae* that emerged from excised, field-collected galls were sexually mature, or nearly so, each female containing many full-size ova. These proovigenic females mated in laboratory cagings from 1 to 7 days-old ($n = 35$) (Fig. 12I). Ten males lived 11.5 ± 0.8 (range, 7–16) days; 11 nonovipositing females, 8.7 ± 0.7 (range, 5–12) days in insectary cagings. These mean longevities fell between the 1-week averages for *P. kristineae* (Silverman and Goeden 1980) and the 3-week averages for *P. stonei* (Green et al. 1993) under similar insectary conditions. This compares with longevities that averaged 42 days for males and 39 and 102 days for two series of synovigenic females ($n = 11$ and 20, respectively) of *P. flavipes* (Goeden et al. 1994a), which has an aggregative life cycle different from the circumnatal life cycles of *P. kristineae*, *P. lisae*, and *P. stonei* (Headrick and Goeden 1994).

The reproductive behavior of *P. lisae* resembled that of *P. kristineae* described by Silverman and Goeden (1980) and by D. H. Headrick from field observations (see below), and that of *P. stonei* described in greater detail by Green et al. (1993). Furthermore, a lack of courtship behavior and exclusive exhibition of enantion type of wing movements by both sexes reported by Headrick and Goeden (1994) as characteristic of circumnatal species of *Procecidochares* also was confirmed for *P. lisae*. Wing enantion as defined and described by

Green et al. (1993) and Headrick and Goeden (1994) was observed for *P. lisae* as males tracked females prior to copulation, during copulatory induction behavior, and following postcopulatory separation. Copulation by only one pair of *P. lisae* was observed from start to finish for 62 min, but nine more partially observed matings all were of shorter duration. Disengagement by three different pairs of adults was observed, whereby the males turned and walked off and away from the females as they concurrently pulled their genitalia from the females' cloacas in one continuous motion in 15, 18, and 30 sec, respectively. The wings of both sexes of *P. lisae* usually were parted at 45° and centered over their midlines during copulation; whereas, Silverman and Goeden (1980) reported that males of *P. kristineae* usually were only slightly parted during copulation, a position sometimes also adopted by *P. lisae* males.

Field observations.—Field observations of *P. kristineae* behaviors on *Ambrosia dumosa* were made by D. H. Headrick at Snow Creek, Riverside Co., 2–9 April 1992. Most observations were made for 1–3 h daily on three large shrubs all bearing newly formed, immature inflorescences.

The oviposition behavior of *P. kristineae* females was highly stereotypical. Each female began by walking from the base of a current season's branch to the base of the raceme, where she turned head-downward, recurved her abdomen and oviscape, and probed with the apex of the aculeus into a leaf axil. After ovipositing or probing, the female moved basally to the next leaf axil and probed or oviposited in the same manner. When the female reached the base of the new growth, she moved to another branch and repeated the above behaviors. Females probed many leaf axils, but oviposited into only 1 to 4 axils per branch. Oviposition times averaged 2 min 9 sec ($n = 4$; range, 2 min–2 min 20 sec). Females frequently stopped to rest and groom between ovipositions.

Mating behavior of *P. kristineae* was

similar to that reported by Silverman and Goeden (1980). Males encountered females either while perched on top of branches or while moving through the crown. Males tracked females slowly from behind. Males sat still in a passive position if the female turned to face him, or paused nearby. Males mounted females by jumping onto their dorsa, either head first or from behind. Once mounted, males clasped the costal margins of the female's wings near the base with the foretarsal claws; the middle legs were wrapped around the middle of the abdomen of the female and the hind legs were bent and crossed underneath the abdomen of the female. Once mounted, males immediately began rubbing their hind legs asynchronously anterior to posterior underneath the abdomen of the female. Simultaneously, the abdomen of the female was raised and the apex of the ovipositor was placed into the epandrium; exertion of the aculeus followed ($n = 5$). Copulation in the field lasted 30 min ($n = 2$).

Seasonal history.—*Procecidochares lisae* usually is univoltine, but occasionally, following substantial late-summer rainfall stimulating renewed host-plant growth, produces a facultative second generation. *Procecidochares kristineae* is normally bivoltine throughout its much wider range in southern California, but as reported by Silverman and Goeden (1980) can locally show univoltine, biennial, and even trivoltine reproduction (unpublished data), depending on whether rainfall locally triggers resumption of gall and larval development concurrent with host-plant regrowth. Both species, along with *P. stonei*, exhibit the circumnatal life cycle defined and described by Headrick and Goeden (1994).

Natural enemies.—The following chalcidoid Hymenoptera were identified as parasitoids of *P. lisae*: *Eurytoma* sp. and *E. veronia* Bugbee (Eurytomidae), as primary, solitary parasitoids reared from mature galls; *Halticoptera* sp. (Pteromalidae), as a primary, internal, larval-pupal parasitoid; *Tetrastichus* sp. (Eulophidae), as a gregar-

ious, puparial endoparasitoid; *Torymus* sp. (*Bedeguaris* group), *Torymus* sp. (*Tubicola* group), *T. capillaceus* (Hüber) (Torymidae), probably as primary, solitary, larval ectoparasitoids as reared from immature galls.

Silverman and Goeden (1980) reported 10 species of parasitic Hymenoptera reared from fully formed galls of *P. kristineae*, an unidentified vertebrate predator of the larvae and identified spider predator of the adults, and two species of inquiline weevils. Green et al. (1993) subsequently reported four species of primary chalcidoid parasitoids individually reared from puparia of *P. stonei* as well as a hyperparasitized larval parasitoid. The genera of parasitoids common to all three *Procecidochares* hosts were *Eurytoma*, *Halticoptera*, and *Tetrastichus*.

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